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Unusual early development in a cyclostome bryozoan from the Ukrainian Miocene

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A b s t r a c t : Recent cyclostome bryozoans possess lecithotrophic larvae which spend a short period swimming in the water column before settlement. Larvae initially attach to a hard or firm substrate, using the adhesive sac, before commencing secretion of the protoecium. This low dome-shaped calcareous structure has a flat underside conforming to the surface of the substrate. Protoecia of similar morphology characterise all previously described fossil cyclostomes as well as extinct stenolaemate bryozoan orders. A large population of a Middle Miocene (Serravallian) cyclostome from the Lower Sarmatian (Volynian) of Polupanivka, Medobory Ridge, western Ukraine is very unusual in having a spheroidal or ellipsoidal protoecium without a flat attachment surface. Colonies of this unidentified tubuliporine are small, infertile, and usually consist of a single, gently curved branch. Larvae are inferred to have undergone metamorphosis and secretion of the calcareous protoecium while unattached and still floating in the water column. It is unknown whether colonies remained in the plankton throughout their inferred short lifespans, or descended to the sea-bed and became free-living benthos. The small size of the colonies, coupled with the lack of gonozooids, suggests that colonies were reproductively inviable, possibly representing the stray offspring of a population of larger fertile colonies that lived and reproduced elsewhere.

K e y w o r d s : Bryozoa, Cyclostomata, Miocene, Ukraine, larval development

Introduction

Most sedentary and sessile benthic animals living in the sea have planktonic larval stages. These larvae are the main vectors of species dispersal and vary greatly between taxa in their residency times within the plankton (JABLONSKI & LUTZ 1983). The larvae of most bryozoans, including all cyclostomes, are lecithotrophic. They are incapable of feeding and are reliant on parental provisioning during their short lifespans which may be just a few hours. No mineralized skeleton has been reported hitherto in the larval stage of any bryozoan – formation of the skeleton commences after larval settlement and metamorphosis on a hard or firm substrate in all described species. This contrasts with some other groups, notably molluscs, where the first parts of the skeleton begin to form before settlement while the larva is still in the plankton.

Cyclostomes are an ancient order of stenolaemate bryozoans which are greatly outnumbered by cheilostomes in modern oceans. Nevertheless, about 850 species of living cyclostomes have been described (HOROWITZ & PACHUT 1996). Larvae are short-lived lecithotrophs in every cyclostome species for which they have been described. According

to NIELSEN (1970) the embryology of all known species is very similar. Primary embryos multiply clonally through embryonic fission inside specialized brood chambers (gonozooids) in adult colonies before being released into the plankton as larvae. The brooded embryos in each gonozooid are clones (HUGHES et al. 2005). Individual larvae are ovoidal, about 100-150 µm in maximum dimension, totally covered by cilia and have a posterior invagination, known as the adhesive sac, and a cuticle-covered apical invagination. There is no trace of the apical organ seen in some other bryozoans, or of the gut which is present in the small minority of cheilostome bryozoan species that have planktotrophic larvae. Upon settlement, the adhesive sac everts and fixes the metamorphosing larva onto the substratum. The apical invagination everts simultaneously, causing the ciliated original outer surface of the larva to become internalized, after which the cilia begin to degenerate. The resulting low dome-shaped structure, variously called the protoecium, proancestrula or primary disc, rapidly commences to secrete a calcified covering from its outer epithelium. WEEDON (1998) described the skeletal ultrastructure of cyclostome protoecia and showed how calcification of the basal layer proceeds centripetally from the outer rim, with the domed roof also calcifying centripetally towards an opening that is the beginning of the main distal tube of the ancestrula.

Numerous examples of dome-shaped protoecia have been figured or described in recent and fossil cyclostomes, as well as bryozoans belonging to extinct stenolaemate orders (e.g. PODELL & ANSTEY 1979), pointing to a broadly similar pattern of larval settlement and metamorphosis across the entire Class Stenolaemata. In all cases, the protoecium is either found still cemented to its substratum (e.g. a shell), or has a flattened basal side where it was formerly attached (cf. TAVENER-SMITH (1974) who described some peculiar conical structures in a Carboniferous cryptostome). It is clear that calcification normally postdates larval fixation in stenolaemates. Here, we describe what appears to be a unique fossil population of a cyclostome in which the protoecium is spheroidal or ellipsoidal, lacks a flattened basal side and can be inferred to have commenced calcification prior to settlement of the larva, contrary to all other known stenolaemates. The colonies, all of which are small and infertile, may have been unattached throughout their short lifespans, possibly floating and entangled among algal threads, or alternatively free-lying on the seabed.

Material and Methods

The material used in this study was collected by one of us (MJ) during 2001-2 from Polupanivka in the central part of the Medobory Hills, western Ukraine. This locality yielded the richest bryozoan fauna among five Miocene bryozoan-bearing localities spread over a distance of ca 150 km from Ternopil to Kamianets Podilskyi (Fig. 1). The samples from Polupanivka were taken from marly and sandy silts that infilled small depressions in the top of a Badenian coralline algal reef.

The sediment from Polupanivka containing the bryozoans is uncemented and required no maceration or other treatment. Picked bryozoans were mounted using adhesive carbon tab backings onto standard SEM stubs and examined uncoated using a LEO 1455VP low-vacuum scanning electron microscope at the NHM. Images were formed using back-scattered electrons rather than the more usual secondary electrons. Scanned specimens depicted in Figures 4-10 are deposited in the collections of the Polish Geological Institute, Warsaw (abbreviated MUZ PIG).

Geological setting

The Miocene in the Medobory area consists of marine Upper Badenian and semi-marine Lower Sarmatian deposits (Fig. 2). Coralline algal reefs are the most prominent Upper Badenian facies. Apart from coralline algae, the reef frameworks have colonies of hermatypic corals and vermetid gastropods, and there is a rich reef-associated biota of bivalves and gastropods, echinoids, crustaceans, foraminifers, bryozoans and serpulids. Various bioclastic, marly and rhodoid facies occur in association with the reefs. The overlying Sarmatian buildups, designated as "serpulid-microbialite reefs", cover the slopes of the Badenian reefs and also form individual mounds called "*tovtra*" mounds. The reefs are composed mainly of calcite precipitates of microbial and inorganic origin, with a minor skeletal framework of serpulid tubes and, in places, bryozoans (JASIONOWSKI et al. 2003a, b). Locally, masses of serpulid-microbialite boundstone are encrusted by coralline algae, bryozoans and foraminifers. The Sarmatian biota is taxonomically impoverished but often rich in individuals, and comprises species of bivalves, gastropods, foraminifers and ostracods typical of a semi-marine environment.

In the Early Sarmatian the Paratethys was a brackish basin due to its restricted connections to the World Ocean and a large excess of meteoric water input over evaporation. The Badenian/Sarmatian boundary marks a drastic reduction in the diversity of bivalve faunas as well as the sudden evolution and dispersal of endemic taxa (STUDENCKA & JASIONOWSKI 2003). Reduction in diversity can also be seen among the bryozoans when comparing Badenian and Sarmatian assemblages in the Medobory region. It seems that the Sarmatian expansion of serpulid-microbialite buildups is related to a peculiar interplay of regional and local factors in this region (JASIONOWSKI 2004). First, the restriction of the entire Paratethyan basin resulted in a brackish water environment inhabited by a depauperate biota while simultaneously enabling the blooming of microbial communities. Secondly, strong evaporation of the brackish water caused supersaturation with respect to calcium carbonate and consequently widespread precipitation of calcite (including calcification of the microbial mats).

Biostratigraphically, the Polupanivka bryozoan locality falls within the Lower Sarmatian (Volhynian), based on the assemblage of foraminifers which includes the age-diagnostic species *Elphidium reginum* (D'ORBIGNY) and *E. josephinum* (D'ORBIGNY), as well as *E. aculeatum* (D'ORBIGNY), *Varidentella reussi* (D'ORBIGNY), *Quinqueloculina* and *Articulina problema* BOGDANOWICZ (see JASIONOWSKI et al. 2003a, c). This is Middle Miocene and equivalent to the Serravallian stage of the global geological timescale. The bryozoans, constituting about 95% of the fauna in the marl, include *Tubulipora dimidiata* REUSS, *T. flabellaris* (FABRICIUS), *Tervia* sp., *Mecynoecia* sp., *Cryptosula terebrata* (SINZOW), and probably a second species of *Cryptosula*, and globular celleporiform colonies possibly belonging to *?Celleporina rostrata* (MALECKI) (see HARA 2003).

Results

Delicate, proximally-tapering branches of an erect cyclostome (Fig. 3) occur abundantly in the bryozoan-rich, basal Sarmatian marl from Polupanivka. Most are less than 3 mm in length, vary in shape from straight to gently curved (Fig. 4) or even S-shaped (Fig. 6), and have branches that are more or less circular in cross-section. Although small, the

colonies mostly appear to be complete and are not fragments of larger colonies that have been broken up. Ramifications are extremely rare and comprise daughter branches that diverge at high angles from the main branch (Fig. 5). The branches are monomorphic, consisting only of autozooids which have slender exterior frontal walls. Gonozooids have not been observed. The terminal apertures of the autozooids are slightly longitudinally elliptical and about 100 µm in diameter. Preserved peristomes are short. Autozooidal apertures do not open around the entire 360° circumference of the branch but instead branches have a barren, reverse side. Distally, apertures are aligned in poorly-defined and irregular transverse groups comprising 3-4 apertures. Pseudopores are not usually visible, probably due to infilling by fine-grained sediment and/or cement.

A high proportion of the branches preserve the ancestrula at the proximal end. This is variable in length, often extremely long and over 1.5 mm (Fig. 7). The first budded zooids originate from the underside of the ancestrula and are usually shorter than it. At the proximal end of the ancestrula is the protoecium (Fig. 8-10). This is marked off from the distal tube of the ancestrula by a slight constriction and has a smooth surface which contrasts with the transversely wrinkled surface texture of the distal tube (Fig. 8-9). Protoecia are bulb-like, usually longer than wide (Fig. 8, 10), but occasionally wider than long (Fig. 9), 90-160 µm long by 100-120 µm wide. The proximal end is rounded, smooth and entire (Fig. 8-9), or alternatively corroded in appearance (Fig. 10) and sometimes pierced by a small hole. Occasionally an annular groove marks off the pristine distal part of the protoecium from the corroded proximal part (Fig. 10). None of the specimens show any indication of flattening of the protoecium against a former substrate of attachment, in contrast to the normal morphology of cyclostome protoecia detached from hard or firm substrates.

Discussion

Identity of the bryozoan

In the absence of gonozooids, the identity of this unusual Miocene cyclostome cannot be established beyond subordinal level. Two cyclostome suborders – Articulata and Tubuliporina – have autozooids with calcified exterior walls but the *Polupanivka* species probably does not belong to the former as there are no indications of socket-like nodes and the autozooidal apertures are less regularly arranged than is customary for the Articulata. Knowledge of gonozooid morphology and location is essential for distinguishing between tubuliporine families, and also genera, but the presence of an exterior-walled branch dorsal surface devoid of autozooid apertures prompts comparisons with such genera as *Exidmonea* DAVID, MONGEREAU & POUYET, *Tervia* JULLIEN, *Nevianipora* BORG and *Decurrella* MONGEREAU & BRAGA. In *Exidmonea* and *Decurrella*, the autozooidal apertures tend to be arranged in more clearly defined rows than is the case for the *Polupanivka* cyclostome, whereas *Nevianipora* has branches flattened in the plane of the dorsal surface, in contrast to the subcircular branch cross sections seen here. *Tervia* seems a more likely candidate – the finding of elongate, dorsal gonozooids that characterize *Tervia* would confirm this possibility.

Early development

As mentioned above, cyclostome protoecia normally have a flat surface where the larva settled and attached itself to a hard or firm substratum. The absence of such a surface in the Polupanivka cyclostome has important implications for the early development of the colony. Instead of commencing calcification after settlement, it appears that the larvae metamorphosed and began secreting the skeleton of the protoecium while they were still afloat. NIELSEN (1970) remarked on the tendency for laboratory reared larvae of some cyclostomes to metamorphose on the water film. However, according to Claus Nielsen (pers. comm. to PDT June 2005) these larvae 'developed as if the water film was a normal substratum, only the "bottom" side was a little convex'. Therefore, the Polupanivka cyclostomes apparently did not metamorphose on the water film but rather in the water column itself.

Figure 11 shows how the normal pattern of metamorphosis after attachment could have been modified in the unattached Polupanivka cyclostome. Eversion of both the adhesive sac and the apical invagination is likely to have occurred in much the same way as for other cyclostomes, except that the adhesive sac was not flattened against a substrate of attachment but instead was outwardly convex, giving the post-larval stage an ovoidal rather than hemispherical shape. As in conventional cyclostomes, calcification probably commenced rapidly after metamorphosis to form the protoecium. The proximal annular groove seen in some protoecia (Fig. 10) may mark the boundary between the proximal part of the protoecium secreted by the everted adhesive sac and the distal part secreted by the apical evagination, with the front of calcification proceeding concurrently in both distal and proximal directions from this boundary. The proximal front of calcification usually closed like an iris diaphragm, sealing this end of the protoecium. However, in some instances closure was incomplete, leaving a hole in the calcified skeleton; this hole would have been covered by cuticle during life. The fully-formed protoecium always retained an open distal end from which the distal tube of the ancestrula grew, in most cases to a very considerable length before terminating in an aperture through which the lophophore could be extended.

Adult ecology

Judging by their small size, the Polupanivka cyclostome colonies lived for only a short period of time. Nevertheless, they were clearly able to survive for long enough to develop not only a complete ancestrula but also to bud ten or more additional zooids in many cases. This amount of post-larval growth indicates that the colonies were certainly capable of feeding – parental provisioning of the larvae to allow such an amount of growth without feeding is inconceivable.

Interpreting the ecology of the small yet functionally feeding colonies from Polupanivka is difficult. A key problem is knowing whether they were benthic (i.e. lived on the sea bed) or planktonic (i.e. lived in the water column). A related issue concerns their possible means of attachment. The great majority of living bryozoans are benthic. Notable exceptions are the spherical planktonic colonies of a species of the soft-bodied ctenostome *Alcyonidium* found floating in the Weddell Sea (PECK et al. 1995), and various pseudoplanktonic bryozoans that live attached to floating seaweeds, shells or plastics (e.g. TAYLOR & MONKS 1997). Colonies of the Polupanivka cyclostome bear no resem-

blance in morphology to the planktonic *Alcyonidium* and are not closely related phylogenetically to this genus. Neither do the Polupanivka colonies show any skeletal evidence of having once been attached to floating objects, such as underside bioimmuration of the form of the substrate.

Many modern cheilostomes employ cuticular rootlets for anchoring adult colonies after initial fixation of the larva is achieved using the everted adhesive sac. In *Scrupocellaria reptans* (L.), however, SILÉN (1980) described how the metamorphosing larva used a sticky secretion and not the adhesive sac to secure itself to the substratum, after which a pair of rootlets were produced to establish a more permanent anchorage. As in the Polupanivka cyclostome, *S. reptans* has an ancestrula with a rounded proximal end. Cuticular rootlets do not occur in cyclostomes and can be safely ruled out as a mode of attachment for the Polupanivka species. However, it is plausible that a similar sticky secretion to that found in *S. reptans* was employed by the larvae of these cyclostomes for initial fixation to unknown substrates. If so then the Polupanivka cyclostome larvae may have undergone metamorphosis immediately above attachment substrates located on the sea bed, with adult colonies adopting a benthic habit but probably resting freely on the sediment surface.

An alternative scenario interprets the Polupanivka cyclostome colonies as planktonic and inhabiting intermediate levels in the water column. While it is possible to envisage the small cyclostome colonies floating freely in the manner inferred for colonies of the extinct hemichordate graptolites (e.g. UNDERWOOD 1993), perhaps a more plausible hypothesis is that they became loosely entangled in filamentous algae which held them aloft. The curved shape of the single-branched colonies may reflect slight adjustments in growth trajectory caused by shifts in the exact orientation of the unstable colonies in the water column.

Whatever the ecology of the adult colonies, the Polupanivka population of this unusual cyclostome appears not to have been reproductively viable. It is impossible to know whether any of the small colonies produced sperm, but the total lack of gonozooids among the large sample of complete colonies is good evidence that they were incapable of brooding embryos or releasing larvae. A reproductively viable population of larger colonies of the species likely existed nearby and supplied the larvae that developed into the small infertile Polupanivka colonies.

In summary, the Polupanivka cyclostome provides the only documented example of a stenolaemate with a protoecium – the first formed part of the skeleton – which is spheroidal or ellipsoidal in shape and lacks the normally flattened surface for attachment to a hard or firm substrate. The larva is inferred to have metamorphosed while still floating in the plankton, the everted adhesive sac having no role in fixation, unlike other cyclostomes and most bryozoans in general. Various scenarios for the post-larval mode of life of the small colonies can be suggested but these are difficult to test decisively using the evidence at hand. Colonies may have been benthic or planktonic. It is possible that the larva initially attached to the substratum using a sticky secretion, as in the cheilostome *Scrupocellaria reptans*, with the adult colonies becoming free-lying members of the benthos. Alternatively, the small colonies could have floated, perhaps entangled in filamentous algae. A source population of reproductively competent colonies is envisaged to have existed nearby as none of the Polupanivka colonies have gonozooids for larval brooding and are therefore inferred to have been reproductively inviable.

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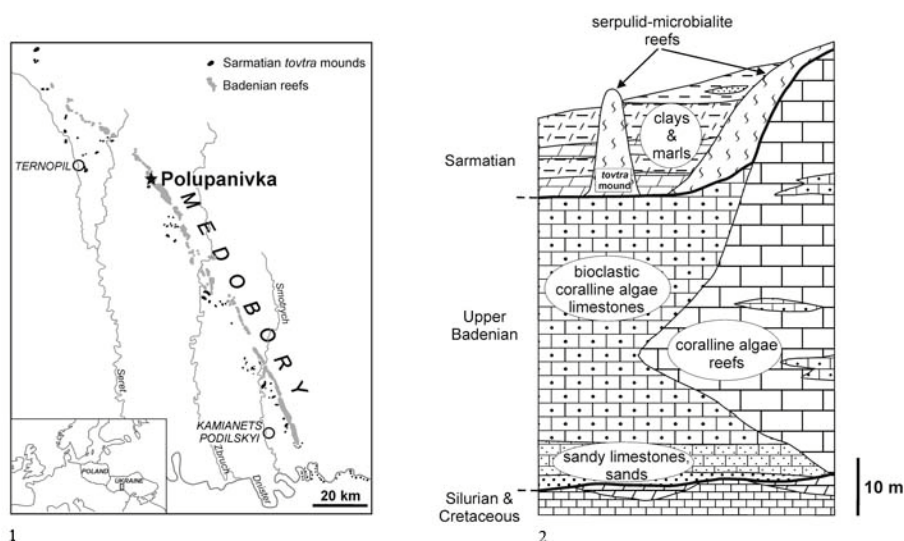


Fig. 1-2. 1: Locality map of the Medobory Hills, western Ukraine (modified from KOROLYUK 1952). 2: Lithostratigraphy of the Miocene deposits in the Medobory area.

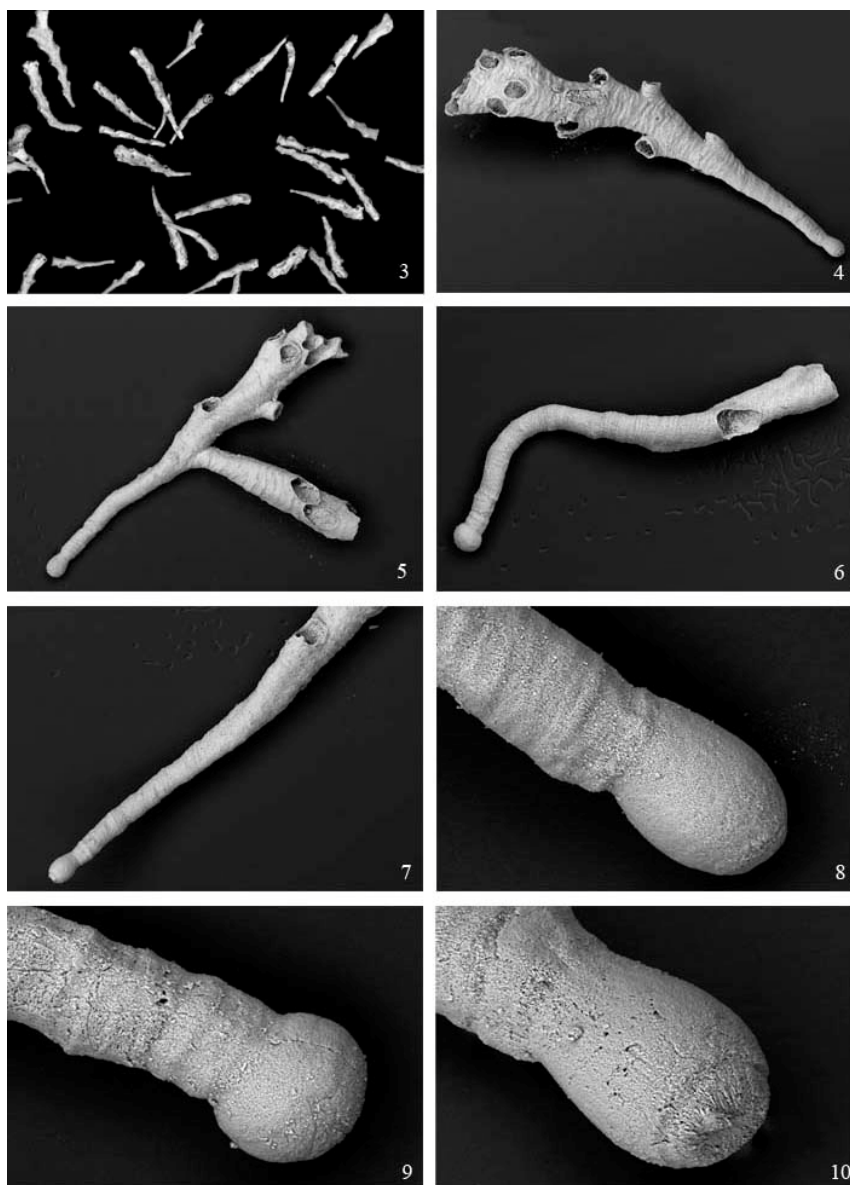


Fig. 3-10. Images of the unidentified tubuliporine cyclostome from the Lower Sarmatian of Polupanivka, western Ukraine. **3:** Scatter of colonies (x 4.7). **4-10.** Back-scattered scanning electron micrographs of uncoated colonies. **4:** Moderately large colony with protoecium (lower right) and growing edge (upper left), Coll. MUZ PIG 1696.II.14 (x 22). **5:** Rare example of branch bifurcation, Coll. MUZ PIG 1696.II.15 (x 24). **6:** Small, sinuous branch, Coll. MUZ PIG 1696.II.16 (x 37). **7:** Extremely long ancestrula, Coll. MUZ PIG 1696.II.17 (x 30). **8:** Typical, longitudinally elongate protoecium, Coll. MUZ PIG 1696.II.18 (x 190). **9:** Transversely elongate protoecium from specimen shown in Fig. 6, Coll. MUZ PIG 1696.II.16 (x 200). **10:** Protoecium with corroded proximal end from specimen shown in Fig. 4, Coll. MUZ PIG 1696.II.14 (x 210).

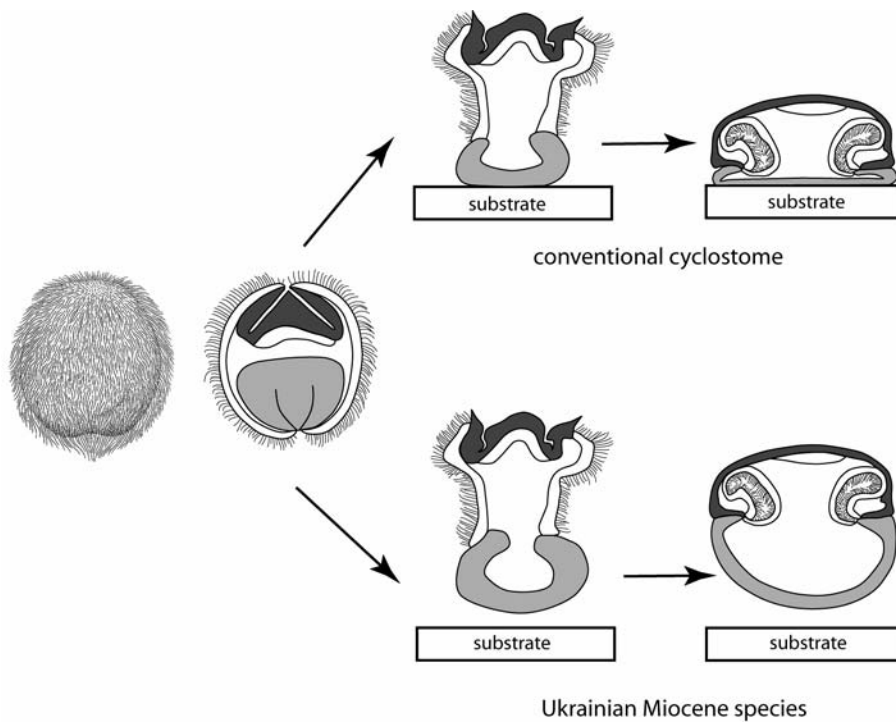


Fig. 11: Model of larval metamorphosis in the Polupanivka Miocene cyclostome compared with a conventional cyclostome (based on NIELSEN 1970: fig. 2, 1995: fig. 24.3). The ciliated larva (far left) is vertically sectioned to reveal the apical invagination (black) and the invaginated adhesive sac (grey). Normally (top row) during metamorphosis the adhesive sac evaginates to attach the larva to a substrate. However, in the Polupanivka Miocene cyclostome (bottom row), evagination of the adhesive sac apparently occurred while the larva was still floating in the plankton and the adhesive sac no role in attaching the larva to a substrate.